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Complex Undisturbed Riparian Zones Are Resistant to Colonisation by Invasive Alien Plant Species

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Abstract: We investigated the presence and abundance of invasive alien plant species (IAS) in the riparian zones of rivers in relation to different environmental parameters. We surveyed the spatial and human-influenced characteristics of the riparian zones, river channels, and land use along seven Slovenian rivers. We further monitored the presence and abundance of IAS with different natural properties and different human impacts to define the characteristics of non-infected and heavily infected reaches. Special attention was given to different life forms of IAS. The presence and abundance of IAS positively correlated with distance from river source, current velocity, and water depth, and negatively correlated with altitude, naturalness of the land use, width and completeness of the riparian zone, height and structure of its vegetation, and condition of the riverbed and banks. Annuals prevailed among IAS at 48%, with 37% herbaceous perennials and 15% woody species. The vine *Echinocystis lobata* was the most abundant IAS, which was found in 179 out of the 414 river reaches analysed, followed by the annual *Impatiens glandulifera* and the herbaceous perennial *Solidago gigantea*. *E. lobata* was spread over the native riparian vegetation and was affected by the natural gradients of the rivers in terms of altitude and distance from the river's source. Reaches without IAS significantly differed from reaches colonised with IAS in the width of riparian zone, vegetation height and structure, land-use next to the river, and distance from the source. As IAS in riparian zones affect riparian and aquatic communities, there is the need for management practices to maintain and establish complex riparian zones that are resistant to IAS colonisation.

Keywords: rivers; riparian zones; Slovenia; central Europe; hydromorphological alterations

1. Introduction

Riparian vegetation is an important part of riverine ecosystems and is essential for their structure and function [1]. The structure of riparian vegetation depends on climate, river hydrology, local geomorphology, and frequency of disturbance [2]. In central Europe, natural riparian zones consist of woody species and herbaceous wetland plant species, which build specific vegetation types [3,4].

Riparian plants are mainly phreatophytes and are rooted in the waterlogged hyporheic zone, which is spreading under and laterally of the waterbody [5]. They are tolerant to flooding, erosion, and sedimentation of eroded material [6]. They have protective functions for watercourses, as they provide a buffer against negative impacts from catchment areas since riparian vegetation reduces the levels of pollutants and nutrients flushed from the catchment areas. The quantity and quality of organic matter entering the river, which supports the aquatic biota, depends on the floristic composition of the riparian vegetation [6–8]. The input of organic matter into a river that derives from riparian vegetation can account for 80% to 95% of the total input mass [6]. The function of riparian vegetation depends on the properties of the riparian zones in terms of their width, complexity, and vegetation type, which are closely related to the ecological status of a river [9,10].

Riparian zones are among the most complex ecological systems of the biosphere. They are often highly productive and diverse parts of the landscape [2]. A large number of species have habitats that include riparian zones, while also providing shelter for species from other parts of the landscape [11–13]. Riparian zones represent the backbone of the natural vegetation or even its last remnants in the agricultural or urban landscapes [14]. Alterations to riparian zones increase their vulnerability, and consequently, that of the rivers, should there be substantial changes in the environmental factors that are essential for the riverine communities [6,15]. So, the conservation of undisturbed riparian zones is essential.

Degradation of riparian zones and its vegetation facilitates the spread of invasive alien plant species (IAS) [16,17]. Introduction of IAS can significantly reduce the fitness and growth of the native plant species [18] which can lead to biodiversity loss, and thus can affect the functions of riparian zones. Besides, also the adjacent areas with inadequate land use can act as sources of IAS [19–21]. In such habitats, the density of available propagules of IAS is much higher in comparison to their natural habitats [22–26]. Positive effects on the spread of IAS can also arise from changes in the riverbed [27,28].

Invasive alien plant species represent a threat to biodiversity [29], as the dominance of IAS in a habitat alters the conditions such that they become less suitable for the native species [30–32]. Different studies have shown that the effects of IAS on aquatic ecosystems structure, and the functions also include changes in the timing and amount of organic matter inputs, the organic matter decomposition rates, and the overall community structure [33].

Although riparian zones represent a small proportion of the landscape, they are often under considerable human pressure due to the interests of many sectors, which poses a huge challenge for their conservation [34]. Despite their great importance, riparian zones are exposed to frequent anthropogenic disturbances in addition to natural disturbances, and these can facilitate the spread of IAS, as these species are adapted to thrive in frequently disturbed environments [35–37]. As well as frequent disturbances, the spread of IAS in riparian zones is facilitated by changes in riverbed structure [38], such as dam construction and watercourse regulation, which both result in alterations of the composition of the riparian vegetation [39]. Furthermore, the removal and thinning of woody vegetation and increased leaching of fertilisers from agricultural areas can create ideal conditions for the promotion and spread of IAS [40]. Indeed, as much as 28.5% of all of the data on IAS in Slovenia are from riparian zones which represents the highest proportion of all habitat types considered [41]. A study by Wagner et al. [42] covering wider area, as well as others (e.g., [43]) also report that riparian ecosystems are among most prone to invasions by IAS.

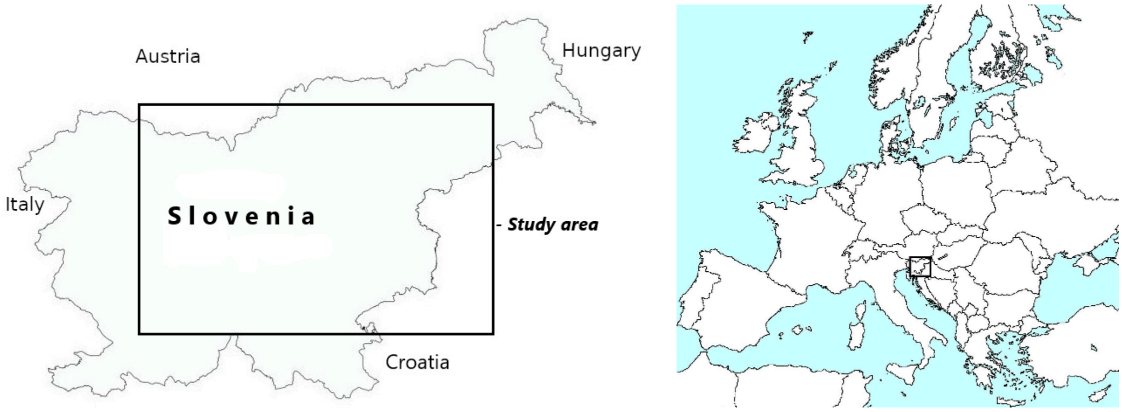
The aim of the present study was to investigate the relationships between the spatial and human-influenced characteristics of riparian zones and their river channels, and the distribution of IAS along sections of seven Slovenian rivers. The questions addressed here were: (a) Do the structural characteristics of riparian zones relate to the presence and abundance of IAS? (b) Do the numbers and abundance of IAS in riparian zones reflect the intensity of anthropogenic disturbance? (c) Does the land use along these rivers differ significantly between infected and non-infected reaches?

On this basis, we hypothesised that: (1) the riparian zones in IAS-dominated reaches will be more disturbed, narrower, and have less-complex vegetation structure; (2) significant changes in land use adjacent to riparian zones and disturbance of the riverbed and river banks will be related to higher numbers and abundance of IAS; and (3) the distance from the river's source will be positively correlated with the numbers and abundance of IAS.

2. Materials and Methods

2.1. Field Survey

The survey was performed along seven rivers in the central Slovenia (Figure 1) that form namely the lower part of the Sava River and its larger tributaries: the Savinja, Krka, Sotla, Sora, Ljubljanica, and Tržiška Bistrica Rivers. These rivers differ according to their slopes, orders, and ecoregions (Table 1), although they are all part of the Danube River catchment area.



(**A**) (**B**)

Figure 1. Geographical position of the study area in Slovenia (**A**, left) and in Europe (**B**, right).

Table 1. The main characteristics of the 414 reaches of the rivers studied. Ecoregions: SP—sub-Pannonian, AL—Alpine, DN—Dinaric. Maximum order of the studied rivers in Slovenia is in accordance with Strahler [44].

River	Altitude (m a.s.l.)		Distance from River's source (km)		Nr. of Reaches	Year of Survey	Length of River in Slovenia (km)	Max. Order of River	Eco-Region
	Max.	Min.	Min.	Max.					
Sava	191	134	158	213	55	2013	221	6	SP
Savinja	779	191	0.1	98	80	2011	99	4	AL, SP
Krka	268	140	0.2	95	100	2012	95	4	DN, SP
Sotla	332	136	1	86	86	2009	90	3	SP
Sora	570	309	3.7	52	42	2012	52	4	AL
Ljubljanica	289	284.5	0.1	28	28	2011	41	4	DN
Tržiška Bistrica	766	371	8.1	27.5	23	2011	27.5	3	AL

We collected data on the presence and abundance of IAS along 100-m-long reaches of the riparian zones. The 100-m reaches of the rivers were ~1 km apart. For each section, the mean altitude and distance from the river's source were determined using the Atlas of the Environment [45]. Geographical positions (GKY coordinate—Eastness; GKX coordinate—Northness) were recorded in the field.

The modified Riparian, Channel and Environmental (RCE) method for ecomorphological evaluation of rivers [46] was used with a four-level scale to assess the various parameters. The four-level scale reflected the naturalness of the assessed parameters to reflect the gradients of these parameters due to human impact and the longitudinal character of the rivers [10]. The highest score (4) represents the most natural conditions/undisturbed by humans, and the lowest score (1) was given to the most altered or disturbed conditions (e.g., [9,47]). These parameters included:

(a) Riparian zone properties: width of RZ vegetation (>30 m/5–30 m/1–5 m/<1 m); completeness of RZ vegetation (complete/breaks at >50 m intervals/breaks at 50 m intervals/disturbances frequent); vegetation structure (riparian trees and/or marshy species/pioneer trees and shrubs/herbaceous species, few trees and shrubs/mainly herbaceous species); vegetation height (trees >4 m high/shrubs up to 4 m/herbaceous plants and shrubs 1–2.5 m/herbaceous plants < 1 m); bank structure (stable, firmly held by roots/firm but loosely held by roots/loose/unstable, easily disturbed); bank erosion (little or none/at curves or constrictions/frequent/in entire reach, banks falling in); bank changes (no visible changes/transverse changes/embankment with natural material/embankment with artificial material).

(b) Channel properties: channel depth (width/depth ratio: <7/8–15/15–25/>25); channel changes (none/deepened or widened/dams from natural materials/dams from artificial material); riffles & pools (at every 5–7 stream widths/irregularly spaced/long pools following short riffles/channel regulated); current velocity (torrential/very fast/fast/moderate/slow/not visible); water depth (>1 m/0.3–1 m/<0.3 m).

(c) Land-use: land-use adjacent to RZ (≤30 m) (forest, wetland/mixed pasture, wood, swamp, arable land/agricultural landscape/urban landscape, with gardens and ruderal areas); land-use in wider catchment area (≤100 m), which was estimated using Atlas of Environment [45].

The surveys were performed in different years (see Table 1) from the last week of July to the end of August, when IAS were fully developed. A four-level scale was used to estimate IAS abundance in each 100-m reach, as: 1, sporadic, with ≤5 specimens; 2, rare (≤20 individuals), with small stands; 3, common (>20 specimens), as multiple stands; 4, dominating the riparian zone, with large monotypic stands.

2.2. Data Analyses

The correlations between the numbers and abundance of IAS and the explanatory variables were tested using Spearman rank correlation coefficients. The analysis was performed using SPSS (version 17). The influence of the environmental factors on the distribution of IAS was tested with canonical correspondence analysis using the Canoco 4.5 programme package [48]. First, detrended correspondence analysis (DCA) was performed, where the eigenvalue for the first axis was 0.56 and the gradient length was 8.1 standard deviations, which defined strong unimodality. Therefore, canonical correspondence analysis (CCA) was performed. The IAS that were present only in one or two reaches were excluded from the analysis. Forward selection was used, where 999 permutations were performed in every round to rank the relative importance of the explanatory variables and to avoid collinearity, as suggested by Hudon et al. [49]. Only the factors where $p < 0.05$ were kept in the further analysis. Statistically significant factors were used to create the CCA diagram. The map of abundances of IAS in reaches was created with QGIS [50].

We compared the river reaches with different abundances of IAS in riparian zone (RZ) to find differences in the environmental parameters. The river reaches were arranged into four groups according to the presence of IAS: (1) IAS absent, (2) IAS present with ≤5 or 5 to 20 individuals were merged into this group, (3) several stands of IAS present, and (4) IAS dominant. The differences in the environmental parameters between these four groups were tested using Kruskall-Wallis tests and Mann-Whitney post-hoc tests.

3. Results

3.1. IAS Frequency, Abundance, Life Forms, and Distributions

A total of 27 different IAS were recorded for the total of 414 reaches of the riparian zones along these seven rivers in Slovenia. Only 38 sections were free of IAS. For the frequency of the different life forms of IAS in reaches, annuals prevailed at 48%, followed by herbaceous perennials (37%). The proportion of woody species was lower, at 15%. The most frequent IAS in these riparian zones was the vine *Echinocystis lobata*, followed by *Impatiens glandulifera*, *Solidago gigantea*, *Erigeron annuus*, *Robinia pseudacacia*, *Helianthus tuberosus*, *Ambrosia artemisiifolia*, *Fallopia japonica*, and *Solidago canadensis*, which were all present in >50 reaches. Other species were much less frequent (Figure 2).

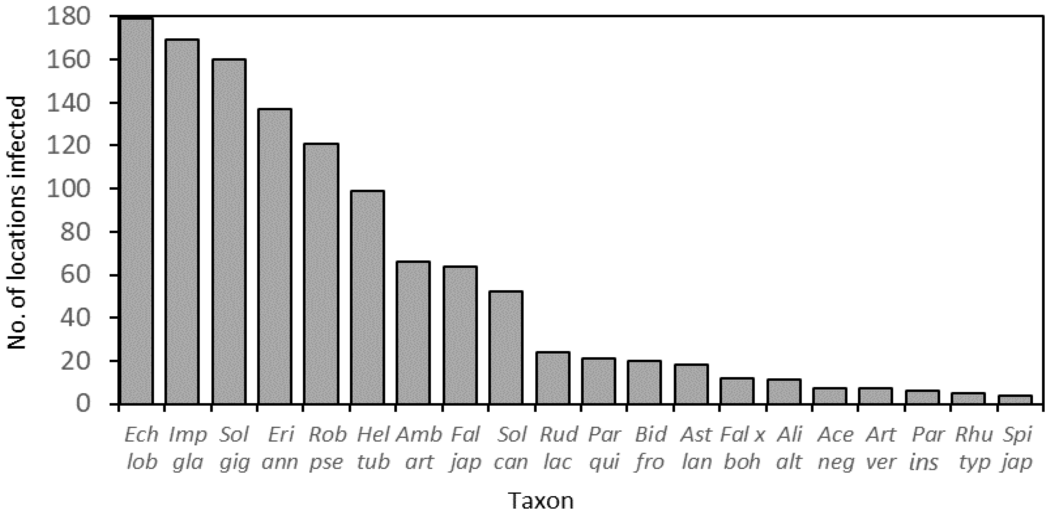


Figure 2. The number of reaches of the riparian zone in which individual IAS were recorded. Abbreviations of scientific names: *Ech lob—Echinocystis lobata*, *Imp gla—Impatiens glandulifera*, *Sol gig—Solidago gigantea*, *Eri ann—Erigeron annuus*, *Rob pse—Robinia pseudacacia*, *Hel tub—Helianthus tuberosus*, *Amb art—Ambrosia artemisiifolia*, *Fal jap—Fallopia japonica*, *Sol can—Solidago canadensis*, *Rud lac—Rudbeckia laciniata*, *Par qui—Parthenocissus quinquefolia*, *Bid fro—Bidens frondosa*, *Ast lan—Aster lanceolata*, *Fal x boh—Fallopia x bohemica*, *Ali alt—Alianthus altissima*, *Ace neg—Acer negundo*, *Art ver—Artemisia verlotiorum*, *Par ins—Parthenocissus inserta*, *Rhu typ—Rhus typhina*, *Spi jap—Spirea japonica*.

Some groups of IAS were especially likely to co-occur. For instance, *F. japonica* and *H. tuberosus* or *I. glandulifera* and *Rudbeckia laciniata* (Figure 3) Also, some species like *Spirea japonica* and *Artemisia verlotiorum* occurred alone within the native vegetation.

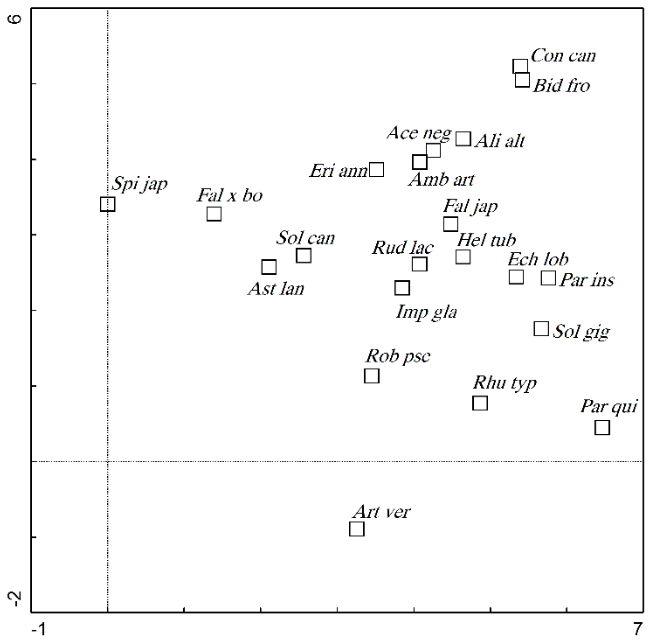


Figure 3. Ordination plot of the detrended correspondence analysis (DCA) that shows the distributions of the individual IAS (excluded: four species in only one section, *Commelina commensis* and *Asclepias syriaca* in only two sections) (for abbreviations see caption of Figure 2).

Abundance gradients of IAS along these rivers seemed very strong in case of the Savinja, Tržiška Bistrica, and Sora Rivers (Figure 4) that flow through the landscape with significant slopes (see Table 1), but were weaker in case of the Ljubljanica, Krka, and Sotla Rivers, which flow through the landscape with gentler slopes. Krka River was the least infected river for IAS.

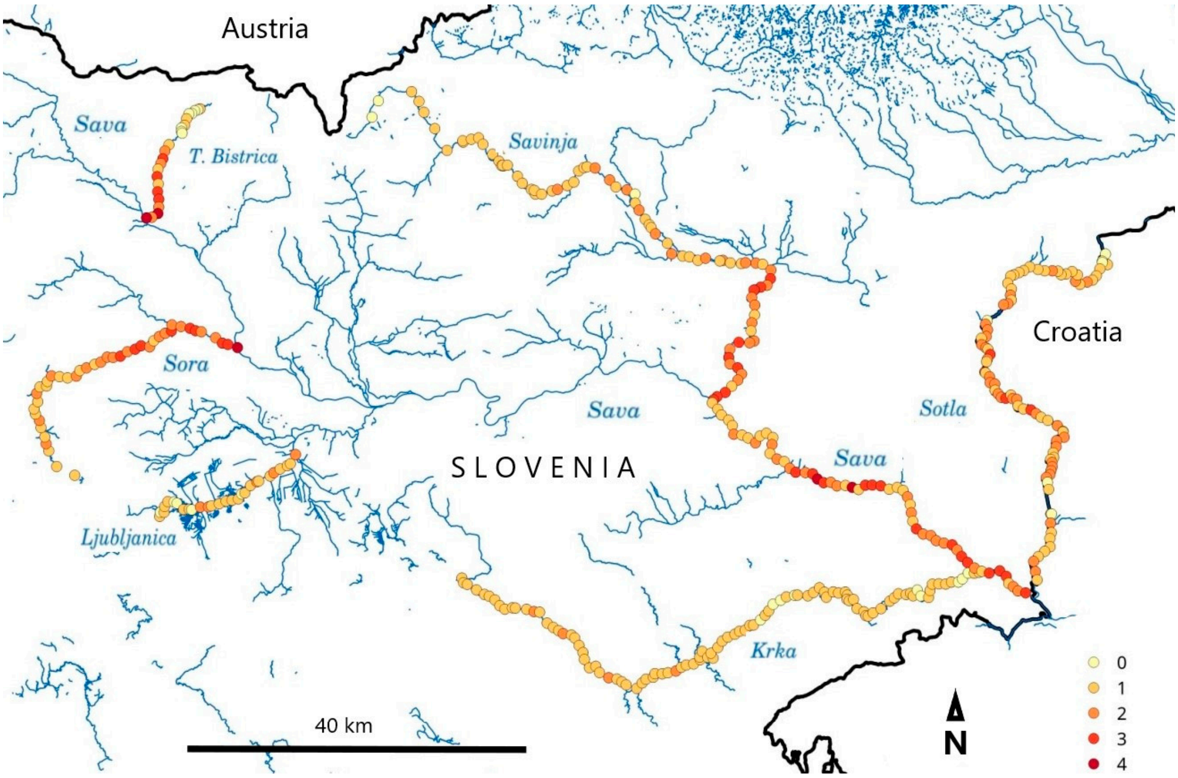


Figure 4. Total abundance for IAS in the individual reaches of the riparian zones analysed along the seven rivers in Slovenia: T. Bistrica, Savinja, Sora, Ljubljanica, Krka, Sotla, and Sava (Key: 1, 1–5; 2, 6–10; 3, 11–15; 4, 16–21) (created with QGIS [50]).

3.2. Relationships Between Environmental Factors and IAS Presence, Abundance, and Form

Correlation analysis for presence, the number, as well as total abundance of IAS showed that the distance from the river's source and riparian vegetation height were the most influential parameters that affected the IAS ($p < 0.05$). The presence of IAS was significantly positively correlated to the distance from the source (Table 2), and negatively to the riparian vegetation height and riverbed naturalness ($p < 0.05$). The same parameters and relations were significant for the IAS total abundance (Table 2). For the different life forms, the most susceptible to morphological alterations appeared to be the annuals. Vines were most affected by the spatial parameters along the longitudinal character of the rivers, which included the water depth and were least affected by the morphological alterations of the rivers (Table 2). Positive correlation was seen between distance from the river's source and current velocity and the number of annual IAS. The riverbed structure was significantly negatively correlated with the number and abundance of herbaceous perennial IAS ($p < 0.05$). The presence of IAS as well as the abundance of herbaceous perennial IAS were negatively correlated with the land use in the wider catchment area and height of vegetation in the riparian zone ($p < 0.05$) (Table 2).

Table 2. Spearman correlation coefficients for the relationships between the environmental factors and the IAS parameters and their growth forms. Shaded fields contain statistically significant correlation coefficients (* at $p < 0.05$; ** at $p < 0.01$).

	Parameter	**Spatial**		**Land Use**		**Riparian Zone Vegetation**				**Banks**		**Channel**			
IAS		**Altitude**	**Distance from Source**	**Adjacent**	**Catchment Area**	**Width**	**Completeness**	**Structure**	**Height**	**Structure**	**Changes**	**Changes**	**Riffles & Pools**	**Current Velocity**	**Water Depth**
All	Total abundance	−0.042	0.332 **	−0.052	−0.090	−0.023	−0.042	−0.029	−0.181 *	0.077	−0.066	−0.138 *	0.027	0.139 *	0.000
	number	−0.061	0.385 **	−0.072	−0.062	0.016	−0.089	−0.062	−0.166 *	0.030	−0.101 *	−0.146 *	−0.040	0.108 *	0.138 *
	presence	−0.074	0.155 *	−0.155 *	−0.158 *	−0.156 *	−0.164 *	−0.131 *	−0.157 *	0.015	−0.068	−0.098 *	−0.008	0.017	0.078
Trees	Total abundance	−0.067	0.082	−0.021	−0.048	0.081	0.074	0.080	0.030	0.062	−0.088	−0.078	−0.072	0.050	0.020
	number	−0.056	0.070	−0.016	−0.037	0.073	0.063	0.071	0.024	0.031	−0.071	−0.063	−0.083	0.034	0.057
Annuals	Total abundance	0.209 *	0.169 *	−0.081	0.027	−0.071	−0.291 **	−0.116 *	−0.172 *	0.122 *	−0.063	−0.072	0.118 *	0.162 *	−0.021
	number	0.179 *	0.177 *	−0.100 *	0.039	−0.056	−0.313 **	−0.164 *	−0.205 *	0.081	−0.099 *	−0.089	0.075	0.123 *	0.050
Perennials	Total abundance	0.000	0.284 **	−0.014	−0.103 *	0.005	0.070	−0.017	−0.157 *	0.060	−0.069	−0.162 *	−0.085	0.132 *	−0.029
	number	0.011	0.341 **	−0.016	−0.086	0.030	0.030	−0.019	−0.128 *	0.052	−0.092	−0.173 *	−0.128 *	0.125 *	0.022
Vines	Total abundance	−0.437 **	0.287 **	−0.076	−0.107 *	0.031	0.083	0.022	−0.019	−0.180 *	0.010	0.020	0.027	−0.156 *	0.254 **
	number	−0.433 **	0.293 **	−0.075	−0.084	0.052	0.096	0.015	−0.005	−0.164 *	0.000	0.010	0.021	−0.163 *	0.245 **

3.3. Impact of Environmental Factors on the Distribution of IAS in the Riparian Zones

The CCA ordination plot shows clusters of these reaches of the seven rivers where the rivers from the central region of Slovenia overlap. However, the three most significant parameters that influenced the distributions of IAS were spatial variables. Single locations within the clusters were distributed along the gradient distance from the river's source. Opposite to this vector, there were gradients of the significant morphological characteristics of the rivers, which showed the pronounced longitudinal character of the rivers (Figure 5). In total, all of the variables explained 17% of the IAS variance. Fourteen of 18 parameters were shown to be significant. The highest share of the variance of the species variability was explained by altitude (4.4%, $p = 0.001$), followed by the distance from source (2.2%, $p = 0.001$), GKY (1.7%, $p = 0.001$), height of vegetation (1.3%, $p = 0.001$), GKX (1.1%, $p = 0.001$), and water depth (0.9%, $p = 0.001$).

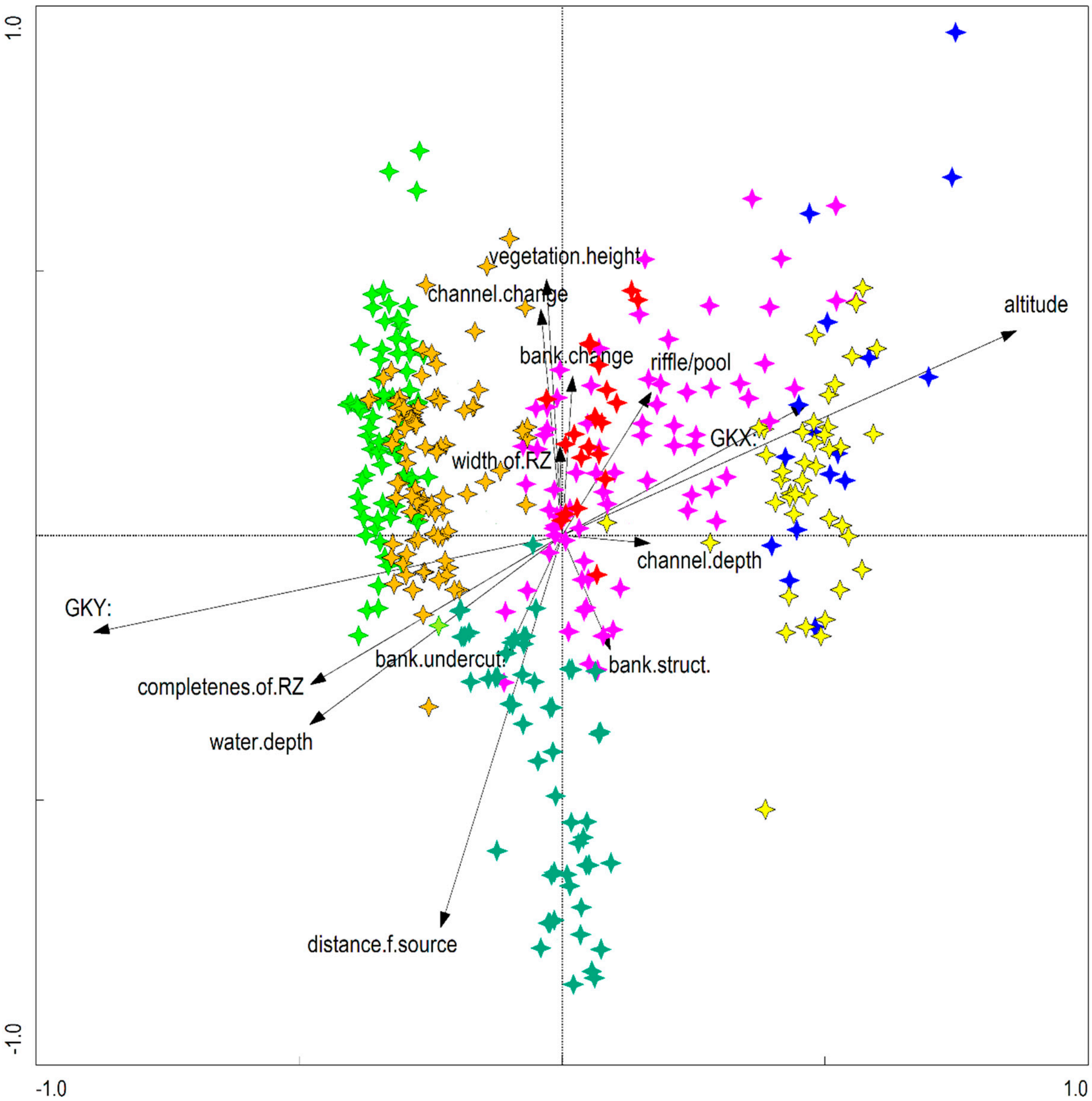


Figure 5. Canonical correspondence analysis ordination plot showing the distribution of the reaches with different abundances of IAS along the significant environmental parameters. Blue, Tržiška Bistrica River; yellow, Sora River; red, Ljubljanica River; pink, Savinja River; orange, Krka River; bright green, Sotla River; dark green, Sava River.

3.4. Comparisons of Reaches with Different IAS Abundance

Significant differences in the abundance of IAS were seen due to different land use adjacent to riparian zones (≤30 m) as well as in the catchment area (≤100 m) (Table 3). The most pronounced differences were obtained between non-infected reaches and all of the other categories. In the non-infected reaches, the land use adjacent to the RZ was significantly less altered than in all of the other reaches (Table 3). Where the riparian zones were at their narrowest, with the least complex native vegetation, the IAS were dominant.

Table 3. Environmental parameters of the river reaches in relation to IAS abundance scores.

Parameter	Specific	1—IAS Absent		2—≤20 IAS Individuals		3—Several IAS Stands		4—IAS Dominant	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Spatial	GKY	501,096	±48,725 ^{ab}	510,244	±36,273 ^{a}	515,831	±47,810 ^{b}	492,717	±52,087 ^{a}
	GKX	104,411	±24,122 ^{a}	90,866	±16,860 ^{b}	100,475	±13,755 ^{ab}	106,636	±12,673 ^{a}
	Altitude (m a.s.l.)	355	±236 ^{ab}	242	±114 ^{a}	229	±99 ^{a}	280	±116 ^{b}
	Distance from source (km)	34	±34 ^{a}	57	±50 ^{b}	76	±64 ^{c}	63	±63 ^{bc}
Land-use	Adjacent	3.5	±1.3 ^{a}	2.7	±1.3 ^{b}	2.7	±1.0 ^{b}	2.8	±0.9 ^{b}
	Catchment	2.9	±0.9 ^{a}	2.3	±1.0 ^{b}	2.2	±1.0 ^{b}	2.2	±0.9 ^{b}
Riparian zone vegetation	Width	3.0	±0.9 ^{a}	2.5	±0.7 ^{bc}	2.5	±0.7 ^{b}	2.3	±0.7 ^{c}
	Completeness	3.5	±0.8 ^{a}	2.6	±1.3 ^{b}	3.1	±1.2 ^{ac}	2.6	±1.3 ^{bc}
	Structure	3.3	±0.8 ^{a}	2.9	±0.9 ^{b}	3.0	±0.8 ^{b}	2.8	±0.9 ^{b}
	Height	3.7	±0.5 ^{a}	3.3	±0.8 ^{b}	3.1	±0.9 ^{bc}	2.9	±1.0 ^{c}
Banks	Structure	3.3	±1.0 ^{ab}	3.4	±0.7 ^{a}	3.4	±0.8 ^{ab}	3.6	±0.8 ^{b}
	Changes	3.6	±0.8 ^{a}	3.3	±1.0 ^{a}	3.4	±0.8 ^{a}	3.3	±1.0 ^{a}
	Erosion	3.1	±0.8 ^{a}	3.5	±0.8 ^{b}	3.4	±0.8 ^{bc}	3.3	±0.9 ^{ac}
Channel	Depth	2.6	±1.2 ^{ab}	2.7	±1.0 ^{a}	3.0	±1.2 ^{b}	3.5	±0.9 ^{c}
	Changes	3.8	±0.6 ^{a}	3.5	±0.8 ^{ab}	3.5	±0.7 ^{b}	3.5	±0.8 ^{b}
	Riffles/pools present	2.6	±1.2 ^{ab}	2.6	±1.1 ^{a}	2.5	±1.3 ^{ab}	2.9	±1.3 ^{b}
	Current velocity	3.2	±1.3 ^{ab}	3.2	±0.8 ^{a}	3.3	±0.8 ^{ab}	3.5	±0.9 ^{b}
	Water depth	2.1	±1.0 ^{a}	2.6	±0.7 ^{b}	2.2	±0.9 ^{a}	2.1	±0.9 ^{a}
IAS	Total number	0	0 ^{a}	2.7	±1.7 ^{b}	3.7	±2.1 ^{c}	3.6	±1.7 ^{c}
	Total abundance	0	0 ^{a}	3.7	±2.5 ^{b}	7.7	±3.5 ^{c}	9.6	±3.7 ^{d}

Different superscript letters indicate statistically significant differences between the four groups of reaches (at $p < 0.05$), according to Mann-Whitney post-hoc test.

4. Discussion

4.1. Presence and Abundance of IAS

High numbers and abundance of IAS were detected in the riparian zones along the rivers studied, which is consistent with many studies [51–54]. Riparian zones are the most fertile and productive parts of the landscape [55] and IAS usually require nutrient rich soil. Zelnik et al. [10] detected the annual species *I. glandulifera* as the most common IAS in the reaches they investigated, followed by *R. pseudacacia* and *S. gigantea*. In the present study, the vine *E. lobata* was the most frequent IAS found. Vines can infect undisturbed riparian zones, as they spread over the native vegetation [10] and thus alter the habitat of the riparian vegetation. Vines are structural parasites that can also affect the architecture of host plants [56] and increase the density of the crowns of native trees, which can make them more prone to breakage under the weight of snow and wind [57].

At least one IAS was present in most of the reaches of these rivers. Among the 414 reaches studied, only 38 were not infected by IAS. The high frequency of IAS in riparian zones can be explained by the frequent and severe natural disturbances caused by floods, bank erosion, and sediment deposition [28,40,41], which all represent a threat to the native vegetation [58].

4.2. Impact of Environmental Factors

Vilà and Ibañez [35] reported more abundant IAS in habitats that were surrounded by a degraded landscape than for those surrounded by a landscape that was close to natural. Zelnik et al. [10] also report a negative correlation between the naturalness of the landscape and the total IAS abundance. We saw significant correlations between land use and total abundance of IAS herbaceous perennials and total abundance of IAS vines. The more natural the land use was, the fewer IAS were present. González-Moreno et al. [26] reported that herbaceous perennials that have clonal distributions with underground stolons [24] are very successful colonisers on disturbed surfaces. The most common herbaceous perennials in the present survey were *S. gigantea*, *H. tuberosus*, *F. japonica*, *F.* x *bohemica*, and *S. canadensis.* The number of IAS annuals was related to land use adjacent to the RZ, and especially that subjected to frequent disturbance [59,60]. The most common tree IAS was *R. pseudacacia*, which contributed the majority (68%) of occurrences of tree IAS. Its negative effect on biodiversity of RZ is enhanced by eutrophication of these sites due to its symbiosis with N-fixing bacteria [61].

Intensive land use has accelerated the spread of IAS also into adjacent natural habitats [21,23,24]. González-Moreno et al. [26] reported that IAS spread through natural habitats was influenced by land use in the adjacent areas, and especially at their edges. This edge effect applies to a relatively large proportion of riparian zones, as they are linear elements of the landscape. These show large edge-to-core ratios, which makes them particularly vulnerable to species invasion from surrounding ecosystems [62].

The vegetation structure and its completeness negatively correlated with the presence of IAS. This is also supported by other studies that have shown that the frequency of IAS is higher where woody riparian vegetation is altered or removed [63,64]. In addition to the vegetation structure, interventions related to the riverbanks can accelerate the spread of IAS [41], namely the removal of the soil and vegetation along with the increase in the light intensity [40].

The number and total abundance of IAS was also related to the riverbed structure, as was shown by Rowntree [38], Merrit and Wohl [39]. The positive correlations between the number of IAS and water depth in the present study are in line with expectations, as water depth affects the extent of the hyporheic zone, and the availability of water for riparian plants [5]. The variable current velocity is usually positively related to altitude and proximity of the source, where in principle, the highest current velocities are recorded (e.g., [65]). Therefore, positive correlations of the current velocity with the number and total abundance of IAS can be indirect. Highly significant positive correlations between the numbers and total abundance of IAS and the distance from the river′s source were calculated. Distance from the source reflects longitudinal gradient [65] as there are constant changes in physical and chemical properties downstream. For instance, current velocity, width of the river, light availability, and accumulation to erosion ratio. The listed changes reflect in the changes of riparian vegetation [66]. There is also a link between distance from river′s source and regime of disturbances driven by spates and floods. Mostly, the intensity of disturbances increases downstream [67], which also explains the higher number and abundance of IAS along downstream reaches (Figure 4). Moreover, river can act as a vector for the spread of IAS propagules, due to its longitudinal character [3] and each settlement might additionally contribute to IAS expansion and directly affect IAS abundance downstream [41,68]. Similar effects might be seen for altitude. Klinger et al. [69] indicated that IAS are less numerous at higher altitudes and increase towards the lowlands. Altitude influences IAS due to the changes in the environmental factors along the altitudinal gradients, such as temperature, water availability, and nutrients [70].

4.3. Comparison of Reaches with Different IAS Abundance

We have shown here that the river reaches without IAS differed significantly from the other reaches on the basis of the following parameters: width of the RZ, height and structure of the riparian vegetation, land use adjacent to the riparian zone and in the catchment area, and intensity of the alterations to the river bed. Thus, in the IAS-free sections, the land use was more natural (e.g., forests, wetlands), the RZ was much wider, and the vegetation was higher and more complex than for the other river reaches with the river bed mainly natural. According to Petersen [46], the land use in the catchment area affects the composition of the riparian vegetation, and thus also the morphology of the riverbed [25]. In the reaches where the IAS dominated the RZ, these were significantly narrower and less complex in comparison to those without IAS. This indicates the need for sufficient width of riparian zones [46] to make them resistant enough to IAS infection [40].

Our study has revealed that complex preserved riparian zones can prevent the establishment and expansion of IAS along rivers. The exceptions here are the alien invasive vines, which can spread more easily over native vegetation of preserved riparian zones.

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